MORPHOLOGICAL VARIATION IN MALUKU POPULATIONS OF SYCONYCTERIS AUSTRALIS (PETERS, 1867) (CHIROPTERA : PTEROPODIDAE)

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ABSTRACT

The skull, dentary, dental and external morphology of populations of *Syconycteris australis* from Ambon, Seram, Kai, Aru, and New Guinea Islands were compared using univariate and multivariate statistics. The Ambon and Seram populations are distinct and recognised as *S. a. major* Andersen, 1911, although it may warrant recognition as a separate species. The Kai Island population is morphologically distinct from those of New Guinea but are conjoined by the Aru Island population. The taxonomic status of the Kai Island population is indeterminate.

INTRODUCTION

Andersen (1912) recognised three species of *Syconycteris*: *S. crassa* (Thomas, 1895) (Maluku islands; New Guinea and associated eastern islands, except Woodlark Island); *S. australis* (Peters, 1867) (Queensland) and *S. naias* (Andersen, 1911) (Woodlark Island). More recently *S. hobbit* Ziegler, 1982 was described from Papua New Guinea and *S. carolinae* Rozendaal, 1984 from NW Halmahera Island.

Tate (1942) reported both *S. crassa* and *S. australis* from New Guinea. However, Lidicker and Ziegler (1968), McKean (1972), Hill (in Greig-Smith 1975), Koopman (1979, 1982) and Ziegler (1982) could find no consistency with diagnostic characters used to separate these species (elongation of PM4 and M1 and presence of M^2 and M_3). Consequently *Syconycteris crassa* is currently considered a subspecies of *S. australis*. The subspecies of *S. australis* recognised by Hill (1983) are as follows (type locality in bold):

S. a. australis (Peters, 1867) - **Queensland**, Australia.

S. a. papuana (Matschie, 1899) - New Guinea; **Andai, NW New Guinea**, Aru I.

S. a. crassa (Thomas, 1895) - SE New Guinea Is; (Tobriand Is; D'Entrecasteaux Is, **Fergusson** I.).

S. a. keyensis Andersen, 1911 - **Kai** Is.

S. a. major Andersen, 1911 - **Ambon** I. and Seram I.

S. a. finschi (Matschie, 1899) - **Bismark Archipelago.**

Hill (1983: 139) considered that the subspecies of *S. australis* "seem only slightly differentiated". This observation explains why McKean (1972) synonymised *keyensis* and *finschi* with *papuana* and regarded *naias* as synonymous with *S. a. australis*. Koopman

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(1982), however, considered *finschi* a subspecies. Hill (1983: 139) suggested that *naias* from Woodlark I. is possibly synonymous with *australis* but "may prove to be another weakly separable subspecies".

There has been no study of the morphology and taxonomic status of the Maluku populations of *S. australis* since Andersen (1912). This paper reports on a univariate and multivariate analysis of the morphology of *S. australis* populations from Seram, Ambon, Kai and Aru islands, Maluku (Figure 1), and makes comparison with populations from Papua New Guinea and Irian Jaya.

MATERIALS AND METHODS

A total of 133 adult specimens (listed in specimens examined section) was examined. These were from Ambon (15), Seram (26), Dullah I. / Kai Kecil (2), Kai Besar I. (37) Wokam I. / Aru islands (13), Irian Jaya (3) and Papua New Guinea (37). The locality of these specimens is shown in Figure 1. All specimens are currently lodged in the Western Australian Museum. The specimens from Indonesia were collected during 1987-1993 by staff from the Western Australian Museum and Museum Zoologicum Bogoriense.

Seventeen measurements of skull, dentary and dental characters and 10 of external characters (all in mm) were recorded from adult specimens.
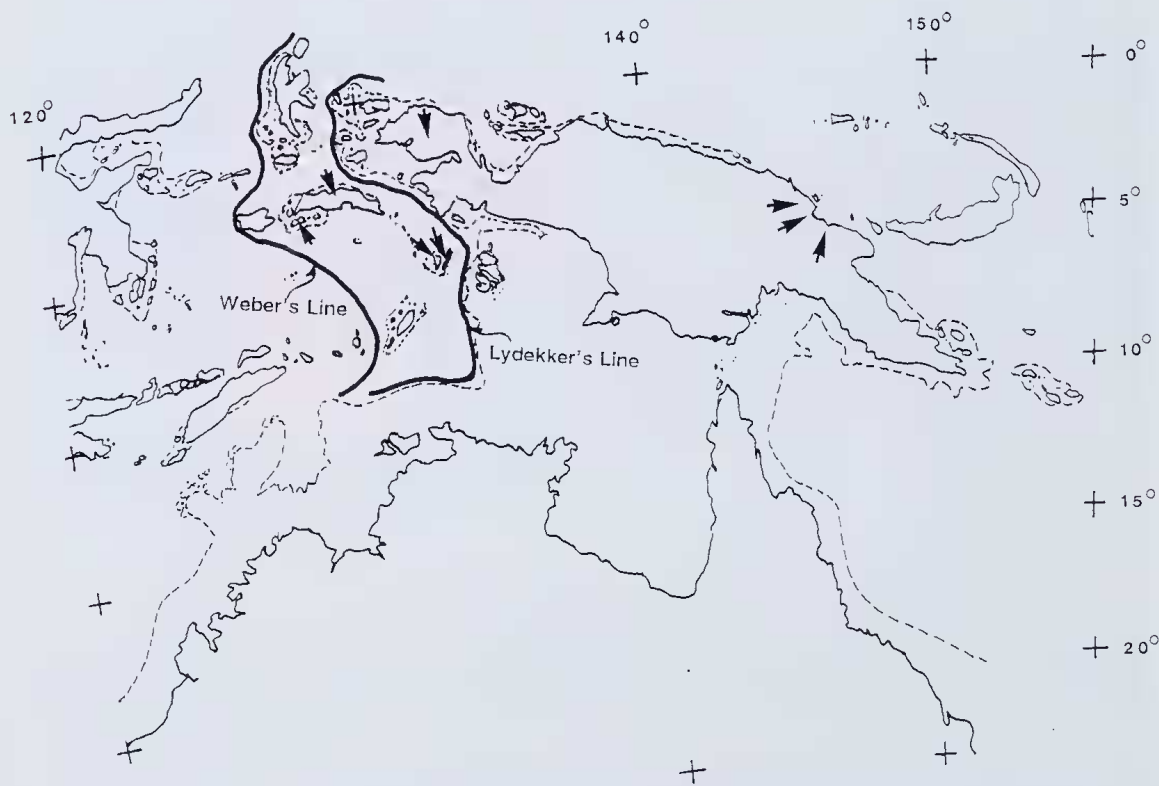
Figure 1   Localities of *Syconycteris australis* specimens used in this study. Also shown are the boundaries of the Sahul Shelf (dotted) and both Weber's and Lydekker's biogeographic lines (broad lines).

The measurements recorded follow those in Kitchener *et al.* (1993). They were (all measurement involving teeth are to alveoli): GSL, greatest skull length; CBL, condylobasal length, PIF, minimum length from posterior margin of incisive foramen to margin of posterior palate; RL, rostrum length, from anteriormost internal margin of orbit to nares; RH, rostrum height, from upper canine alveoli to level of dorsal surface of nasals; BB, braincase breadth above zygoma; ZW, zygomatic width; M^1M^1 and C^1C^1, width across M^1M^1 and C^1C^1 respectively, from the labial side; C^1M^1 and C_1M_2 upper and lower canine to last molar length; IOB, minimum interorbital breadth; POB, minimum postorbital breadth; MFW, mesopterygoid fossa width, at the widest point of the palatal flange; P^4P^4, palatal width between the lingual aspect of P^4P^4; ML, mandible length, from condyle to anteriormost point of dentary; CH, dentary coronoid height; SV, tip of rhinarium to anus length; EAR, basal notch to apex length; FA, forearm length; MC3-5, metacarpal 3,4 and 5 length. D3P1-3, digit 3 phalanx 1, 2 and 3 length and TIB, tibia length.

The skull, dentary and dental characters were measured to 0.01, while the external characters were measured to 0.1. Terminology used in the description of skull, dentary, dental and external characters follows Hill and Smith (1984).

Adults were diagnosed as those specimens with the following sutures fused: basioccipital - basisphenoid, basisphenoid - presphenoid and palatine - maxillary.

The effect of sex and island for all characters was examined by standard multiple regressions (where all effects were assessed simultaneously) for the five islands: Ambon, Seram, Kai (Kecil and Besar combined), Aru, and Papua New Guinea. Irian Jaya was excluded because of the small sample size. Examination of the residuals from regression analyses gave no indication of heteroscedasticity.

Because of the large number of interactions being tested the level of significance is taken at $P<0.01$.

A discriminant function analysis was run for skull, dentary and dental characters and external characters using all characters and a reduced set of these characters. This reduced set of characters was selected because they provided values that minimise Wilk's Lambda.

RESULTS

Univariate statistics

The sample size, mean, standard deviation, maximum and minimum values for skull, dentary, dental and external characters of the Ambon, Seram, Kai, Aru, Papua New Guinea and Irian Jaya populations are presented in Table 1a,b (males and females combined). These descriptive statistics show that the Ambon and Seram populations average larger in all skull and external measurements from the other populations, but particularly in the following:

Greatest skull length 28.83 (27.85-29.90) *v.* 25.55 (24.13-27.02), minimum length from incisive foramen posterior margin to posterior palate margin 11.74 (11.03-12.60) *v.* 10.21 (9.46-10.97); mandible length 21.55 (20.69-22.65) *v.* 18.69 (17.37-20.59); C_1M_1 length 9.50 (8.89-10.36) *v.* 8.09 (7.09-8.90), forearm length 48.2 (45.6-50.3) *v.* 42.6 (39.6-46.8) and tibia length 19.3 (17.9-20.9) *v.* 16.9 (15.0-18.3).

The multiple regression analysis of the main effects of sex and islands and the interaction between sex and island showed that the dominant effects were due to differences between the islands (Table 2). All characters were significant at $p<0.001$ between islands, except digit 3 phalanx 3 length ($F_{5,80} = 1.311$, $p=0.273$, NS) and postorbital breadth ($F_{4,80} = 4.314$, $p=0.003$).

Table 1 Measurements, in mm, for (a) skull, dentary, dental and (b) external characters (see Materials and Methods for explanation of character codes) of adult *Syconycteris australis* from Ambon Island, Seram Island, Kai Islands, Aru Islands, Papua New Guinea and Irian Jaya. N, sample size; SD, standard deviation; min., minimum; max., maximum.

Table 1a Skull, dental and dentary

LOCALITY		GSL	CBL	PIF	RL	RH	BB
	N	11	11	11	11	11	11
	MEAN	28.71	27.29	11.57	8.80	3.55	11.67
AMBON	STD	0.42	0.55	0.27	0.30	0.08	0.20
	MIN	27.97	26.49	11.03	8.40	3.46	11.44
	MAX	29.36	28.38	11.97	9.31	3.73	12.03
	N	26	25	26	26	26	26
	MEAN	28.88	27.44	11.81	9.06	3.61	11.72
SERAM	STD	0.51	0.56	0.33	0.35	0.13	0.27
	MIN	27.85	26.27	11.21	8.32	3.34	11.30
	MAX	29.90	28.60	12.60	9.80	3.87	12.29
	N	37	36	37	37	37	37
SERAM/	MEAN	28.83	27.39	11.74	8.98	3.59	11.70
AMBON	STD	0.48	0.55	0.33	0.35	0.12	0.25
	MIN	27.85	26.27	11.03	8.32	3.34	11.30
	MAX	29.90	28.60	12.60	9.80	3.87	12.29
	N	11	11	11	11	11	11
	MEAN	25.44	24.12	10.25	7.34	3.13	11.16
ARU	STD	0.61	0.51	0.28	0.31	0.12	0.32
	MIN	24.44	23.17	9.98	6.84	2.83	10.62
	MAX	26.49	25.06	10.82	7.85	3.29	11.66
	N	31	30	32	31	31	32
	MEAN	25.48	24.17	10.13	7.51	3.11	10.94
KAI	STD	0.45	0.48	0.29	0.29	0.14	0.32
	MIN	24.45	23.17	9.49	6.78	2.82	10.39
	MAX	26.25	25.09	10.90	8.14	3.41	11.68
	N	3	3	3	3	3	3
	MEAN	24.52	23.16	9.74	7.14	2.91	10.56
IRIAN	STD	0.35	0.32	0.25	0.16	0.08	0.11
JAYA	MIN	24.13	22.81	9.58	7.00	2.82	10.46
	MAX	24.80	23.44	10.03	7.32	2.98	10.68
	N	33	32	37	37	37	37
	MEAN	25.74	24.37	10.30	7.63	3.25	10.88
PAPUA	STD	0.74	0.70	0.39	0.44	0.26	0.34
NEW	MIN	24.14	23.03	9.46	6.71	2.75	10.04
GUINEA	MAX	27.02	25.85	10.97	8.58	3.59	11.58
PAPUA	N	78	76	83	82	82	83
NEW	MEAN	25.55	24.21	10.21	7.53	3.17	10.93
GUINEA/KAI/	STD	0.65	0.62	0.35	0.38	0.21	0.34
ARU/IRIAN	MIN	24.13	22.81	9.46	6.71	2.75	10.04
JAYA	MAX	27.02	25.85	10.97	8.58	3.59	11.68

Table 1a (cont.)

ZW	M¹M¹	C¹C¹	C¹M¹	IOB	POB	MFW	P⁴P⁴	ML	CH	C₁M₁
11	11	11	11	11	11	10	11	11	11	11
17.36	6.97	5.87	7.58	6.31	7.17	3.54	5.02	21.35	8.54	9.14
0.69	0.27	0.26	0.28	0.17	0.39	0.13	0.24	0.41	0.52	0.23
16.50	6.58	5.44	7.11	5.98	6.61	3.38	4.65	20.69	7.69	9.09
18.40	7.44	6.13	8.09	6.53	7.77	3.85	5.48	22.13	9.42	9.91
26	25	26	26	26	26	25	25	26	24	26
17.16	6.91	5.70	7.63	6.03	7.00	3.56	5.07	21.63	8.57	9.54
0.64	0.27	0.23	0.28	0.34	0.45	0.14	0.32	0.48	0.44	0.34
15.97	6.49	5.22	7.17	5.42	6.16	3.35	4.39	20.71	7.86	8.89
18.25	7.49	6.21	8.20	6.53	7.91	3.86	5.63	22.65	9.50	10.36
37	36	37	37	37	37	35	36	37	35	37
17.22	6.93	5.75	7.62	6.11	7.05	3.56	5.05	21.55	8.56	9.50
0.65	0.27	0.25	0.27	0.32	0.43	0.14	0.29	0.47	0.46	0.31
15.97	6.49	5.22	7.11	5.42	6.16	3.35	4.39	20.69	7.69	8.89
18.40	7.49	6.21	8.20	6.53	7.91	3.86	5.63	22.65	9.50	10.36
11	11	11	11	11	11	11	11	11	11	11
15.34	6.24	4.98	6.68	5.20	6.69	3.27	4.54	18.86	7.11	8.24
0.43	0.20	0.23	0.27	0.24	0.28	0.17	0.19	0.41	0.33	0.23
14.40	5.94	4.78	6.20	4.91	6.28	3.04	4.19	18.08	6.67	7.85
16.05	6.60	5.36	7.09	5.57	7.24	3.59	4.79	19.52	7.67	8.62
30	32	32	32	31	31	28	32	32	32	30
15.21	6.06	4.96	6.63	5.55	6.76	3.24	4.45	18.59	7.20	8.03
0.53	0.23	0.22	0.24	0.27	0.38	0.11	0.21	0.43	0.36	0.23
14.10	5.56	4.49	5.90	4.95	5.89	2.98	4.06	17.50	6.55	7.55
16.11	6.48	5.36	6.99	5.94	7.44	3.52	4.97	19.43	8.16	8.40
3	3	3	3	3	3	3	3	3	2	3
13.44	5.53	4.44	5.95	4.61	6.55	3.15	4.06	17.57	5.57	7.43
0.19	0.12	0.10	0.16	0.17	0.39	0.11	0.11	0.29	0.25	0.33
13.31	5.40	4.36	5.80	4.44	6.12	3.06	4.00	17.37	5.39	7.09
13.66	5.62	4.56	6.12	4.78	6.88	3.27	4.19	17.90	5.75	7.74
37	36	37	37	37	37	37	37	36	36	36
14.72	6.21	4.94	6.68	5.13	6.70	3.41	4.49	18.81	6.81	8.16
0.83	0.41	0.35	0.50	0.45	0.39	0.20	0.29	0.77	0.44	0.52
13.06	5.19	4.16	5.80	4.34	5.80	2.92	3.89	17.52	6.14	7.11
16.13	6.87	5.52	7.53	5.93	7.79	3.89	5.03	20.59	7.74	8.90
81	82	83	83	82	82	79	83	82	81	80
14.94	6.13	4.94	6.53	5.28	6.72	3.32	4.47	18.69	6.97	8.09
0.77	0.35	0.30	0.42	0.43	0.37	0.19	0.26	0.64	0.48	0.42
13.06	5.19	4.16	5.80	4.34	5.80	2.92	3.89	17.37	5.39	7.09
16.13	6.87	5.52	7.53	5.94	7.79	3.89	5.03	20.59	8.16	8.90

Table 1b Externals

| LOCALITY		SV	EAR	FA	MC3	D3P1	D3P2	D3P3	MC4	MC5	TIB
AMBON	N	11	11	11	11	11	11	11	11	11	11
	MEAN	61.8	16.5	47.8	38.1	27.0	30.3	0.6	37.7	38.0	19.5
	STD	2.6	0.6	1.7	1.3	1.2	1.3	0.2	1.5	1.5	1.0
	MIN	57.2	15.3	45.6	36.1	25.8	28.3	0.3	35.1	35.8	17.9
	MAX	65.4	17.3	50.3	40.3	29.1	31.9	1.1	40.2	40.6	20.9
SERAM	N	23	23	23	23	23	23	23	23	23	23
	MEAN	63.3	16.9	48.5	38.4	27.2	30.8	0.7	38.1	38.9	19.2
	STD	3.7	0.6	1.0	0.9	0.8	1.0	0.2	0.6	0.9	0.5
	MIN	55.3	16.0	46.7	36.7	25.9	28.3	0.2	37.0	37.2	18.2
	MAX	70.0	17.8	50.0	40.0	28.5	32.6	1.0	39.4	40.7	20.1
AMBON/ SERAM	N	30	30	30	30	30	30	30	30	30	30
	MEAN	62.8	16.8	48.2	38.3	27.2	30.6	0.7	38.0	38.6	19.3
	STD	3.4	0.6	1.3	1.1	0.9	1.1	0.2	1.0	1.2	0.7
	MIN	55.3	15.3	45.6	36.1	25.8	28.3	0.2	35.1	35.8	17.9
	MAX	70.0	17.8	50.3	40.3	29.1	32.6	1.1	40.2	40.7	20.9
ARU	N	11	11	11	11	11	11	11	11	11	11
	MEAN	53.1	15.4	42.6	33.0	23.4	26.6	0.6	32.8	33.6	16.5
	STD	4.2	0.7	1.3	1.0	0.8	1.1	0.1	1.1	1.0	0.7
	MIN	48.4	14.1	41.3	31.7	22.5	25.4	0.5	31.5	31.8	15.6
	MAX	62.3	16.2	44.7	34.5	25.0	28.8	0.9	34.9	35.4	17.6
KAI	N	30	30	30	30	30	30	30	30	30	30
	MEAN	54.5	15.3	42.0	33.1	23.7	27.1	0.6	32.6	32.7	16.6
	STD	2.9	1.0	1.0	0.9	0.9	1.2	0.2	0.9	1.2	0.6
	MIN	48.8	14.0	39.6	31.6	21.9	24.3	0.2	34.6	30.7	15.0
	MAX	60.8	17.8	43.9	35.1	26.1	29.7	1.1	34.5	35.6	17.6
IRIAN JAYA	N	3	3	3	3	3	3	3	3	3	3
	MEAN	49.8	15.4	41.5	32.2	23.9	25.2	0.7	31.5	31.4	17.4
	STD	5.2	0.1	0.9	0.1	0.6	0.9	0.2	0.3	0.4	0.6
	MIN	45.5	15.3	40.6	32.2	23.2	24.3	0.5	31.2	31.0	16.8
	MAX	55.6	15.5	42.3	32.3	24.4	26.0	0.8	31.8	31.8	18.0
PAPUA NEW GUINEA	N	36	36	36	36	36	36	36	36	36	36
	MEAN	52.1	16.5	43.2	33.6	24.1	26.9	0.6	33.0	33.2	17.2
	STD	3.5	0.7	1.4	1.2	0.8	1.4	0.2	1.4	1.8	0.7
	MIN	45.4	15.2	40.3	30.9	22.3	24.4	0.2	29.8	27.6	15.5
	MAX	63.6	18.0	46.8	36.1	25.6	29.5	1.0	35.5	36.4	18.3
ARU/KAI/ IRIAN JAYA/ PAPUA NEW GUINEA	N	80	80	80	80	80	80	80	80	80	80
	MEAN	53.0	15.8	42.6	33.3	23.9	26.9	0.6	32.8	33.0	16.9
	STD	3.6	1.0	1.4	1.1	0.9	1.3	0.2	1.2	1.5	0.7
	MIN	45.4	14.0	39.6	30.9	21.9	24.3	0.2	29.8	27.6	15.0
	MAX	63.6	18.0	46.8	36.1	26.1	29.7	1.1	35.5	36.4	18.3

The only characters that differed significantly (p<0.01) between the sexes were braincase breadth ($F_{1,80}$ = 10.871, p=0.001), distance outside the upper canines ($F_{1,80}$ = 12.984, p=0.001) and tibia length ($F_{1,80}$ = 10.255, p=0.002). There were no significant interactions between sex and island.

Canonical variate (discriminant) analysis

Both sexes were combined for these analyses after excluding the characters that were shown above to be sexually dimorphic (BB, C¹C¹ and TIB).

The analysis was carried out separately for skull (plus dentary and dental) and external characters on the remaining 14 skull and 9 external characters, using the islands (Ambon, Seram, Kai, Aru and Papua New Guinea) as the *a priori* groupings; Irian Jaya was unallocated because of its small sample size (N=2). The association between these islands in discriminant function space was very similar for both skull and external characters.

The analysis was run for the 23 skull and external characters using the island groupings above (Irian Jaya unallocated) and again for a reduced set of seven characters (greatest skull length, GSL; rostrum height, RH; interorbital breadth, IOB; cranial height, CH; upper canine to M¹ length, C¹M¹; ear length, EAR and digit 3 phalanx 1 length) that were selected to minimise the values of Wilk's lambda. The reduced set of seven characters gave a very similar
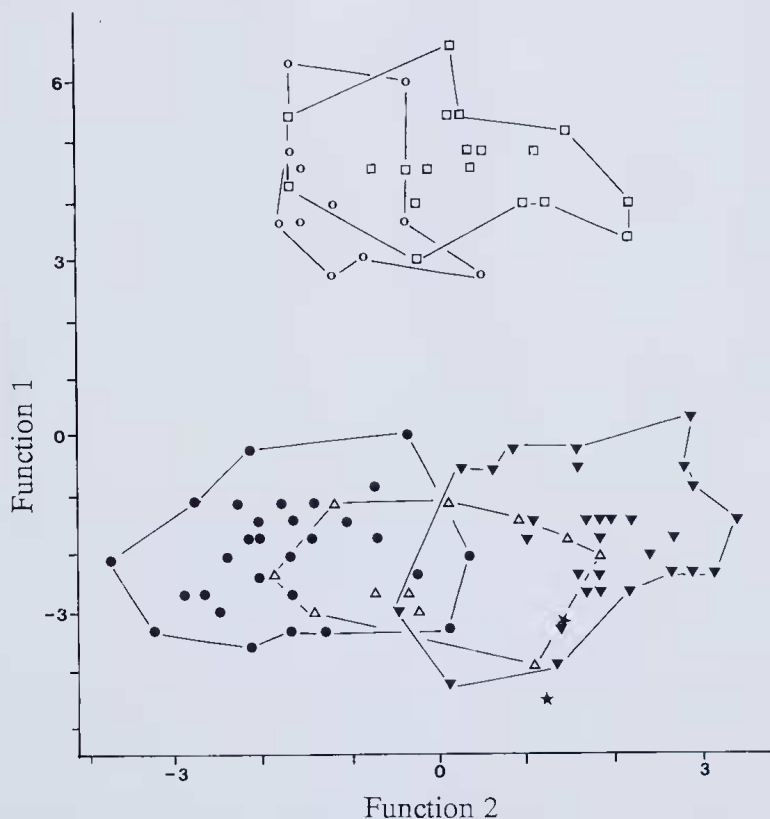
Figure 2   Canonical variate (discriminant) plots of functions 1 and 2 for male and female adult *Syconycteris australis* grouped by locality: Ambon Island (O), Seram Island (□), Kai Island (●), Aru Island (Δ), Papua New Guinea (▼) and Irian Jaya (★).

Table 2 Multiple regressions on sex and localities of *Syconycteris australis* (Ambon Island, Seram Island, Kai Islands, Aru Islands, Papua New Guinea) for skull, dentary, dental and external characters. F values are presented for the main effects and their interaction. For explanation of character codes see Materials and Methods section. Significance levels are *, $0.05>p>0.01$; **, $0.01>p>0.001$; ***, $p<0.001$.

Character	Main Effect		Interaction
	sex	island	sex. island
GSL	0.006	144.465***	1.056
CBL	0.091	130.384***	0.818
PIF	2.076	93.448***	0.326
RL	0.244	78.306***	1.169
RH	1.418	24.982***	0.082
BB	10.871**	30.616***	0.481
ZW	4.396*	9.322***	0.192
M^1M^1	0.005	28.750***	0.164
C^1C^1	12.984**	43.431***	0.824
C^1M^1	0.179	42.885***	0.099
IOB	0.034	25.693***	0.248
POB	0.418	4.314**	0.473
MFW	6.439*	14.505***	0.929
P^4P^4	0.218	22.875***	0.118
ML	1.158	111.063***	0.643
CH	4.828*	52.122***	1.463
C_1M_1	0.933	61.032***	0.181
SVL	0.800	37.461***	0.257
EAR	0.317	15.819***	0.434
FA	1.108	92.887***	2.718*
MC3	0.203	108.445***	2.747*
D3P1	1.691	68.632***	2.249
D3P2	0.008	38.256***	1.165
D3P3	5.520*	1.311	1.418
MC4	1.342	102.280***	2.260
MC5	0.433	68.099***	1.269
TIB	10.255**	66.793***	2.933
Degrees of freedom	1,80	4,80	4,80

pattern of association between these islands in discriminant function space. Because the total number of characters (23) greatly exceeds the sample size in these island groupings (e.g. Aru, N=11 - Irian Jaya is unallocated), the DFA presented and discussed below is that for skull and external characters using the reduced set of seven characters.

The DFA produced three significant functions, with function 1 explaining 80.2% of the variation; function 2, 17.9% and function 3, 1.5%.

The plot of functions 1 and 2 (Figure 2) shows two distinct groupings: first, Ambon and Seram and secondly, Kai, Aru and Papua New Guinea - with the unallocated Irian Jaya clustering close to Papua New Guinea. There are no misclassifications of individuals between these two broad groupings. These two broad groupings separate on function 1. The only character with DF coefficients loading heavily (>0.5) on function 1 is greatest skull length (Table 3), suggesting that it is overall skull size that differentiates these two broad groups. There appears also to be subtle shape differences in the skull of the Ambon and Seram

animals, compared to those of Kai, Aru, Papua New Guinea and Irian Jaya. For example, both their condylobasal length is greater relative to C^1M^1 length (Figure 3) and greatest skull length is greater relative to mesopterygoid fossa width (Figure 4). Within these broad groups the clusters for Ambon and Seram broadly overlap (Figure 2), with a total of 22% of individuals misclassified between Ambon and Seram.

Within the second group (Kai, Aru and Papua New Guinea) the Kai population is separate in DFA space from that of Papua New Guinea, with only 1 out of 60 (2%) of individuals misclassified between these two populations. The Aru population, however, overlaps both the Kai and Papua New Guinea populations. Of the 11 Aru individuals, one was misclassified to the Kai population and two to the Papua New Guinea population (a total of 27.3% misclassified). The separation between the Kai and Papua New Guinea populations was on function 2 (Figure 2). The characters with DF coefficients loading heavily (>0.5) on function 2 were interorbital breadth (0.99), rostrum height (0.85) and ear length (0.59) (Table 3), suggesting that subtle differences in skull shape and ear length partially differentiate these populations. This is confirmed by Figure 5 which indicates that the rostral height is greater relative to interorbital breadth for the Papua New Guinea (and Irian Jaya population) than it is for the Kai population; the Aru population is intermediate.
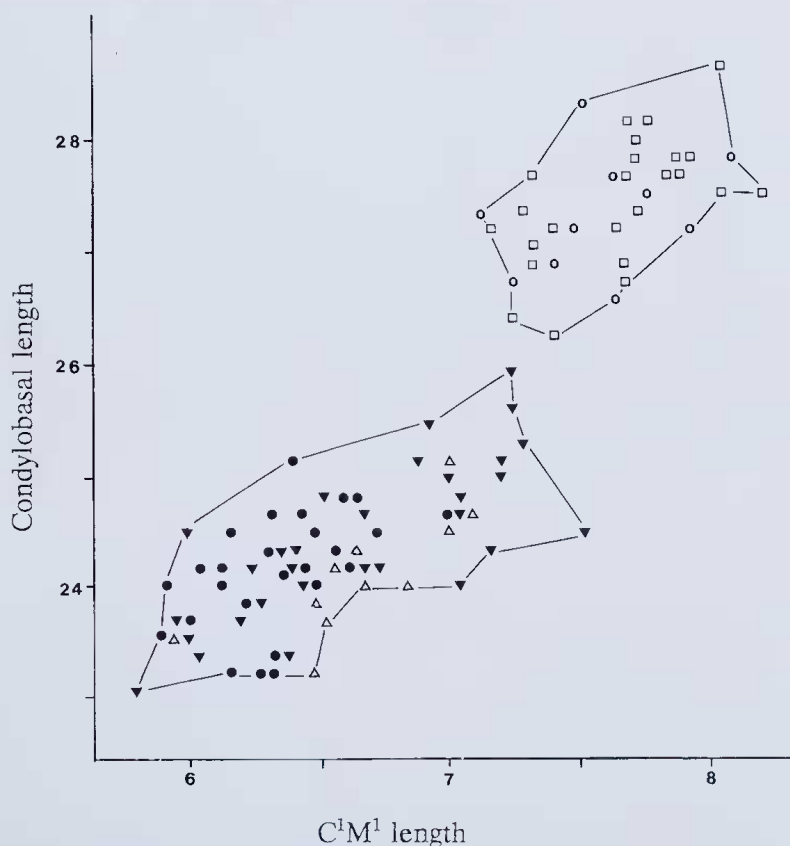
Figure 3   Plot of condylobasal length *versus* C^1M^1 length for *Syconycteris australis* from Maluku and New Guinea. Locality codes as for Figure 2, caption.
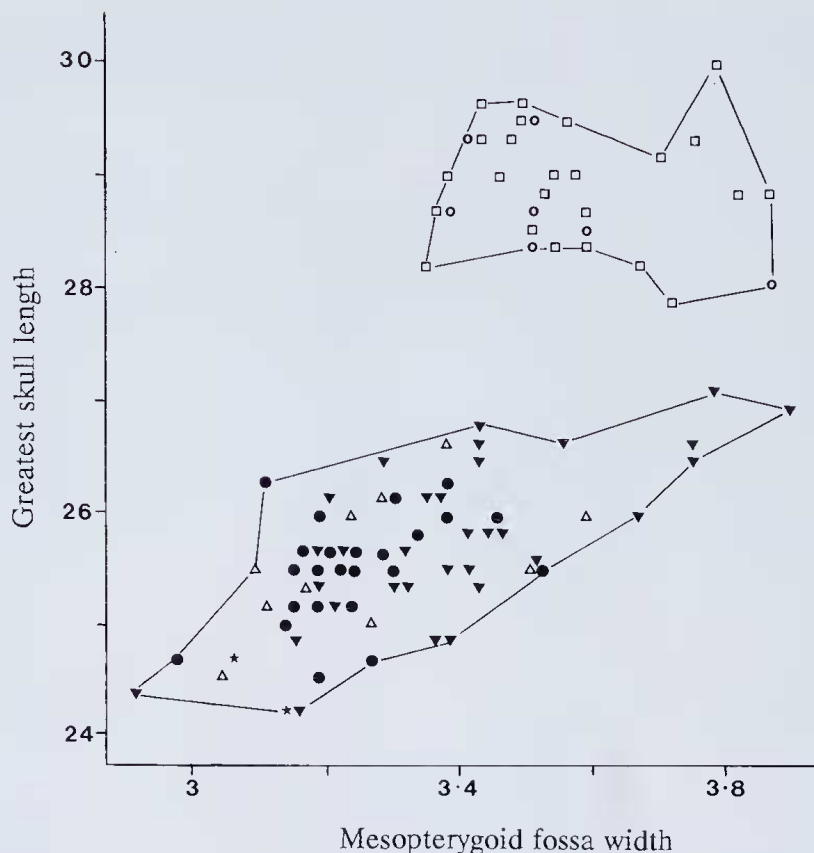
Figure 4 Plot of greatest skull length *versus* mesopterygoid fossa width for *Syconycteris australis* from Maluku and New Guinea. Locality codes as for Figure 2, caption.

Further, the Ambon and Seram population have a greater skull length relative to mesopterygoid fossa width than do the Kai Island, Aru Island and New Guinea populations (Figure 4).

DISCUSSION

Andersen (1912: 781) noted that the Ambon and Seram form (*major*) was the largest of the subspecies of *S. australis*. He stated that "in point of size there may be an absolute, though in any case small, difference between *major* and its nearest geographic neighbour, *papuana* (New Guinea); but *crassa* (Tobriand and D'Entrecasteaux islands) is intermediate".

The Kai Island form (*keyensis*) is almost separate in discriminant function space from *papuana* from Papua New Guinea. Further, it averages smaller in many measurements from the Papua New Guinea form (but not from the few specimens from Irian Jaya) and may be distinguished from the Papua New Guinea and Irian Jaya form by skull shape differences (Figure 5). Andersen (1912) considered the Kai form *keyensis* to be similar in every respect to *papuana*, except for the slightly shorter toothrows. There is no evidence from this study that

Table 3 Canonical variate function coefficients for *Syconycteris australis* from the following locality groups (Ambon Island, Seram Island, Kai Islands, Aru Islands and Papua New Guinea). Standardised values, followed by (in brackets) unstandardised values. For explanation of character codes see Materials and Methods section.

Character	Function 1	Function 2	Function 3
GSL	0.7284(1.2525)	-0.1540(-0.2648)	0.0238(0.0409)
IOB	-0.0169(-0.0480)	-0.9953(-2.8365)	0.6079(1.7325)
RH	0.0383(0.2121)	0.8489(4.6987)	0.2019(1.1178)
EAR	0.0923(0.1225)	0.5907(0.7838)	0.4170(0.5533)
CH	0.2885(0.6333)	-0.3592(-0.7885)	-0.4171(-0.9155)
C^{1}M^1	-0.1121(-0.3171)	0.4682(1.3250)	-0.8358(-2.3650)
D3P1	0.3592(0.4110)	0.0153(0.0175)	0.3713(0.4248)
Constant	-48.4798	-8.9695	-10.8148
Variation explained (%)	80.2	17.9	1.5
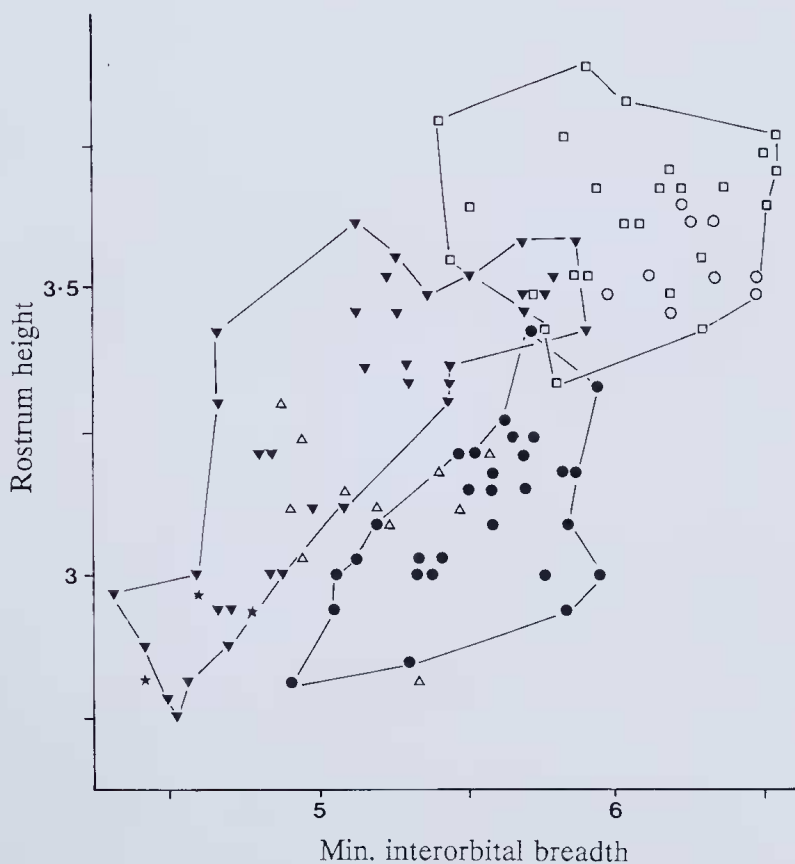
Figure 5 Plot of rostrum height *versus* interorbital breadth for *Syconycteris australis* from Maluku and New Guinea. Locality codes as for Figure 2, caption.

the toothrows of *keyensis* [6.63 ± 0.24 (N=32)] are significantly shorter than those of *papuana* from Papua New Guinea [6.68 ± 0.50 (N=37)] or Irian Jaya [5.95 ± 6.12 (N=3)] (t_{67} = 0.54, p>0.5 and t_{33} = 0.19, p>0.5, respectively).

The Aru Island specimens are considered to be *S. a. papuana* by Andersen (1912). This study shows them to be intermediate and to have measurements that overlap with both those of specimens from Kai and Papua New Guinea (Table 1).

This study shows that in the western part of its distribution *S. australis* has differentiated into a form on Ambon and Seram (*major*) that is quite distinct morphologically and which may in fact be specifically distinct from the forms on New Guinea, Aru and Kai Islands.

The population on Kai Island has been described as subspecifically distinct (*keyensis*) from the New Guinea form (*papuana*). This study confirms this distinction but records that the Aru Island population overlaps morphologically both the Kai Island and Papua New Guinea populations. This may be explained by several processes. First, the Kai population may have resulted from a filtered dispersion pattern from Papua New Guinea through Aru; as such the Kai form is the end point in a morphological cline and probably does not warrant subspecific recognition from the New Guinea population. Secondly, the Kai population is morphologically and taxonomically distinct from the New Guinea form and that both these forms exist on Aru; or thirdly, the Aru form is a hybrid between the Kai and New Guinea forms. Answers to these questions are difficult to obtain from a morphological approach such as this one, and will depend on future genetic studies.

Recently Kitchener *et al.* (1993) highlighted the importance of the zone between Lyddeker's and Weber's Line to an understanding of the processes that determine the interface between the southern parts of the Australian and the Oriental biogeographic regions. In an almost parallel study to this one on *Nyctimene albiventer*, Kitchener *et al.* (1993) noted that while the Aru Island population of *N. albiventer* was morphologically very similar to those of Papua New Guinea, those of Kai Island (and Banda Island) were clearly subspecifically distinct. This paper indicates again that Kai Island populations have differentiated morphologically somewhat from their conspecific populations on the Australian and New Guinea continental shelf.

SPECIMENS EXAMINED

Papua New Guinea

Maiwarva (4°55'S, 145°47'E), 2 unsexed, WAM M26281-2; *Nabanob* (5°09'30"S, 145°45'00"E), 6♂♂ 7♀♀, WAM M27492-3, M27497-8, M27501, M27503, M27556-7, M27560-1, M27564, M27572, M27574; *Nokopo* (5°57'S, 146°36'E), 2♂♂ 6♀♀, WAM M27509, M27542-6, M27549, M27554; *Duvi* (5°56'S, 146°37'E), 1♀, WAM M27514; *Duvi-Nokopo* (5°56'S, 146°36'E), 2♂♂ 3♀♀, WAM M27516-7, M27520, M27531, M27539; *Sempi* (5°00'40"S, 145°46'40"E), 1♀, WAM M27580; *Baumina* (5°29'S, 145°43'E), 1♀, WAM M27584; *Bundi* (5°45'S, 145°14'E), 1♂ 9♀, WAM M27592, M27595, M28505; *Baiteta* (5°00'20"S, 145°44'40"E), 1♂, WAM M28519; *Usino* (5°33'50"S, 145°21'20"E), 1♀, WAM M28522; *Papua New Guinea* (5°30'S, 145°30'E), 1 unsexed, WAM M28529.

Irian Jaya

Porokma (4°00'S, 138°43'E), 1♂ 2♀♀, WAM M29092-4.

Seram Island

Kanikeh (3°00'S, 129°00'E), 11♂♂ 7♀♀, WAM M34167, M34173-5, M34181, M34184-5, M34191-2, M34193, M34205, M34208, M34210, M34214, M34216, M34219, M34227, M34259; *Solea* (2°53'S, 129°32'E), 5♂♂ 3♀♀, WAM M34228-9, M34231-2, M34235, M34238, M34247, M34252.

Ambon Island

Desa Amahusa (3°41'S, 128°10'E), 9♂♂ 6♀♀, WAM M38771, M38773-6, M38779, M38806, M38810, M38850-1, M38853-6, M42363.

Kai Besar Island

Tual and *Fakoi* (*ca.* 5°39'S, 132°59'E), 15♂♂ 21♀♀, WAM 42055-61, M42077, M42093-4, M42096-7, M42110, M42112-3, M42136-7, M42692-3, M42695-8, M42701, M42814-7, M42868-75.

Kai Kecil Island

Near Taman Anggrek, Pulau Dullah (5°38'S, 132°44'E), 1♂ 1♀, WAM M42647-8.

Aru Islands

Karangguli, Wokam Island (05°48'S, 134°15'E), 6♂♂ 7♀♀, WAM M42464, M42483, M42543, M42545-7, M42553-4, M42560, M42573, M42575, M42582-3.

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REFERENCES

Andersen, K. (1911). Six new fruit bats of the genera *Macroglossus* and *Syconycteris*. *Ann. Mag. nat. Hist.* (8) **7**: 641-643.

Andersen, K. (1912). *Catalogue of the chiroptera in the collection of the British Museum 2nd ed. I. Megachiroptera*. British Museum, Natural History, London.

Greig-Smith, P.W. (1975). Notes on a collection of bats and their ectoparasites from the Sepik District, Papua New Guinea. *Sci. New Guinea*, **3**:117-122.

Hill, J.E. (1983). Bats (Mammalia : Chiroptera) from Indo-Australia. *Bull. Br. Mus. nat. Hist. (Zool.)* **45**: 103-208.

Hill, J.E. and Smith, J.D. (1984). *Bats, a natural history.* British Museum, Natural History, London.

Kitchener, D.J., Packer, W.C. and Maryanto, I. (1993). Taxonomic status of *Nyctimene* (Chiroptera: Pteropodidae) from the Banda, Kai and Aru Island, Maluku, Indonesia - implications for biogeography. *Rec. West. Aust. Mus.* **16**: 399-418.

Koopman, K.F. (1979). Zoogeography of mammals from islands off the north-eastern coast of New Guinea. *Amer. Mus. Novit.*, **2690**: 1-17.

Koopman, K.F. (1982). Results of the Archbold Expeditions No. 109. Bats from Eastern Papua New Guinea and the East Papuan islands. *Amer. Mus. Novit.*, **2747**: 1-34.

Lidicker, W.Z. and Ziegler, A.C. (1968). Report on a collection of mammals from eastern New Guinea, including species keys for fourteen genera. *Univ. Calif. Publs Zool.* **87**: 1-60.

McKean, J.L. (1972). Notes on some collections of bats (Order Chiroptera) from Papua-New Guinea and Bougainville Island. *Tech. Pap. Div. Wildl. Res. C.S.I.R.O. Aust.* **26**: 1-35.

Matschie, P. (1899). *Die Fledermäusse des Berliner Museums für Naturkunde. 1. Lieferung. Die Megachiroptera des Berliner Museums für Naturkunde.* Berlin.

Peters, W. (1867). [Herpetologische Notizen]. *Mber. Preuss. Akad. Wiss.* **13**, footnote.

Rozendaal, F.G. (1984). Notes on macroglossine bats from Sulawesi and the Moluccas, Indonesia, with the description of a new species of *Syconycteris* Matschie, 1899 from Halmahera (Mammalia: Megachiroptera). *Zool. Med. Leiden* **58**: 187-212.

Tate, G.H.H. (1942). Results of the Archbold Expeditions No. 48. Pteropodidae (Chiroptera) of the Archbold collections. *Bull. Amer. Mus. nat. Hist.* **80**: 331-347.

Thomas, O. (1895). On some mammals collected by Mr Albert Meek on Fergusson Island, D'Entrecasteaux group. *Novit. Zool.* **2**: 163-166.

Ziegler, A.C. (1982). The Australo-Papuan genus *Syconycteris* (Chiroptera : Pteropodidae) with the description of a new Papua New Guinea species. *Occas. Pap. Bernice P. Bishop Mus.* **25**: 1-22.